On the Paleontology of Animal Cognition: Using the Brain Dimensions of Modern Birds to Characterize Maniraptor Cognition

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Abstract: Drawing inferences on the characteristics, including behavior, of extinct species using comparisons with extant species has a long tradition in paleontology. Departing from the observation that extinct maniraptors possessed brains with a relatively long and narrow telencephalon, we used digital endocasts taken from 11 species of modern birds to determine if any of the sampled modern bird species displayed a similar telencephalic shape, and by inference, similar cognitive ability. The analysis revealed that the telencephalon of the double-crested cormorant (*Phalacrocorax auritus*) is extraordinarily narrow (large length-to-width ratio) and strikingly similar to *Archaeopteryx* and even some non-avian, maniraptoran dinosaurs. The relatively narrow brain in turn suggests a relatively small nidopallium subdivision of the telencephalon and associated impoverished general cognitive ability. This first-order brain-anatomical observation, together with the relatively ancient origins of a cormorant fossil record, suggest that cormorants could be used as a model for the general cognitive abilities of extinct maniraptors.

Keywords: Brain endocasts, Comparative cognition, Double-crested cormorant, Hippocampus, Nidopallium, Paleoneurology.

INTRODUCTION

Considerations of the richness of animal cognitive abilities have been characterized by periods of undisciplined enthusiasm as well as periods of almost complete denial of any cognitive ability at all. For example, after reading Romanes' enjoyable *Animal Intelligence* [1], one cannot help but assign to both vertebrate and invertebrate animals an expansive cognitive ability and even what one might call "mental experiences". But with the subsequent ascendency of Behaviorism for much of the 20th century, the notion of animal cognition fell into disrepute as all changes in behavior were explained in a framework of associative learning. The modern legitimization of research into animal cognition can probably be traced to the watershed contributions of Donald Griffin toward the end of the 20th century [2].

But what do we mean by "cognition" or "cognitive ability"? We do not pretend that one can operationalize such loosely used terms, but in our view, the crucial distinction is that cognitive ability implies a capacity for problem solving or computational facility that cannot be explained on the basis of associative learning no matter how complex the associative learning may be. Although research on mammals, particularly primates, has provided some of the best known examples of animal cognition, observations and experimental evidence from birds have also offered some extraordinary examples of cognition [3]. For example, a New Caledonian crow spontaneously fashioning a rod as a hook to access food [4] or the use of a cognitive map by a homing pigeon spontaneously carrying out a corrective re-orientation following some navigational error can, in our view, both be considered "cognitive" [5].

Any conversation about cognition necessarily raises questions on the permissible properties of brain organization that enable cognition. Here, comparisons between birds and mammals are particularly telling as both groups have evolved hypertrophied forebrains, but the cognition-enabling organization of those forebrains is very different. For example, in primates it can be assumed that the prefrontal cortex, together with its connections to body-centric regions of the parietal cortex and emotion-regulating areas of the limbic system, is taken as the essential brain system that supports cognition. Therefore, the absence of a neo(iso) cortex in birds could then lead one to deny a similar level of cognitive complexity. However, as already noted, research in a variety of bird species over the last twenty years or so belies the notion that a prefrontal cortex is necessary for cognition [*e.g.*, 4, 6]. In fact, the functional properties of the nidopallium [7, 8] of the avian forebrain are remarkably similar to the mammalian prefrontal cortex, suggesting convergent evolution in designing, but not necessarily the design, of a neural architecture that can support cognition.

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The avian hippocampus can also contribute to a conversation on the possibility of studying a "paleontology of cognition". Undoubtedly more than any other brain structure, the hippocampus has shaped conversations in the growing field of neuroecology, which attempts to relate variation in neural organization as an evolutionary outcome of differences in selective pressure associated with different behavioral-ecological challenges. In birds, there is considerable variation in relative hippocampus size, and this variation has been correlated in closely related taxonomic groups with respect to food-caching, nest parasitism and migratory behavior [9]. Although perhaps somewhat simplistic, the general conclusion that emerges from such comparisons is that superior spatial cognitive ability in the context of remembering where food has been hidden, the location of potential host nests or navigating to remote goal locations is associated with a larger hippocampus. These observations render permissible the idea that inferences on relative cognitive ability can be made based on brain morphology.

The issue we would like to raise in this contribution is whether some of the neurobiological approaches that have been used to understand taxonomic variation in cognitive ability in extant species can be used to address the perhaps fantastic question of cognitive ability in extinct animals, and specifically maniraptoran dinosaurs. Much like the question of animal cognition described above, the presumptive behavioral complexity of some herbivorous and predatory dinosaur species has undergone a revision from characteristically slow and highly reflexive/stereotyped to the possibility of being socially complex and intelligent [*e.g.*, 10]. This is particularly true of theropod dinosaurs, and maniraptors in particular. Maniraptor dinosaurs were more closely related to birds than the famous large-bodied carnivores like *Tyrannosaurus rex* (Figure **1**), and studies have shown that endocranial design transitioned within the theropod clade from a crocodilian form to the modern avian model [11-14]. Oftentimes in paleontology modern animals are studied as a proxy for extinct relatives. Because non-avian maniraptors are the sister group to modern birds, we propose there may be an extant avian model that could offer insight into the cognitive ability of extinct maniraptors.

BEHAVIORAL-NEURAL PALEONTOLOGY

Questions about the behavioral complexity and cognition of extinct animals are difficult to answer because paleontologists can only recover skeletal material that has been fossilized in rock and cannot observe behavior directly. Despite this limitation, there are many ways to study the behavior of fossil animals. For example, fossil trackways occur when an animal leaves footprints in loose sediment like sand or mud [15]. If a footprint remains undisturbed as more sand is deposited, then the footprint remains as an observable feature in the rock. In the past, several fossil trackways oriented in the same direction have led researchers to propose that non-avian theropods at least occasionally moved as a social group, reflecting an unexpected degree of social complexity [15-17].

Another source of information on the behavior of extinct animals are death assemblages. A death assemblage refers to a fossil site containing many different animals (often conspecifics) from the same habitat. In the Pleistocene tar pits near Los Angeles, the assemblage of fossil mammals bears a striking resemblance to the community structure found on the African savannah today. In an innovative study, Carbone *et al*. [18] attracted predators to the sounds of dying herbivores and concluded that the composition of the predators attracted to the sounds in Africa had a characteristic social structure, and when compared to the tar pit fossil assemblage, supported the hypothesis of the saber-toothed tiger (*Smilodon*) as a social predator. This study illustrates the potential of using the behavior of living animals to draw inferences on the behavior of animals long extinct.

Closer to our question of the behavior and cognition of non-avian theropods, several recent fossil finds have provided evidence that some theropods were gregarious during at least part of their life cycle. Ibiricu *et al*. [19] described a death assemblage of the small Patagonian coelurosaurian theropod, *Aniksosaurus darwini*, from the Late Cretaceous (about 90 million years ago). At least five individuals appear to have lived and died together; notably all were juvenile to subadult at death. Similarly, Varricchio *et al*. [20] investigated a remarkable bone bed from the Late Cretaceous of Inner Mongolia. Here, over twenty individuals of the ornithomimosaur, *Sinornithomimus dongi*, perished when they became trapped in the muddy shoreline of a small lake. Based on bone histology, all the individuals were juveniles between one and seven years old. It may be that, in at least some non-avian theropods, mature adults and hatchlings stayed together, while older juveniles formed their own social groups.

In addition to trackways and fossil assemblages, fossil cranial anatomy can provide evidence of

cognitive abilities in extinct animals. Paleoneurology is the study of brain evolution in fossil vertebrates. The brains of ancient organisms can be difficult to study because the soft tissues of the head degrade long before a vertebrate can become fossilized. However, paleontologists can reconstruct the soft tissue structures in the cranial cavity (*i.e*., open space in the skull which houses the brain) in different ways, for example, by using the cranial cavity as a mold to fashion an "endocast" [21]. More recently, computed tomography has been applied to create digital, 3D models of fossil endocasts [22, 23]. Although a plaster or digital endocast reveals little with respect to the internal organization of a brain, it does provide data on shape and size, allowing some inference with respect to overall cerebrotype.

As noted above with respect to the avian hippocampus, brain or brain region size is often taken as a proxy for "power", and is probably best exemplified by the classic brain-size to body-size allometric function (encephalization quotient) of Jerison [24], which revealed that behaviorally more complex mammals and birds have generally larger relative brain sizes compared to the other vertebrate groups. The same approach can also be used to assess endocast similarities among closely related groups, even for extinct animals. Modern birds are now generally recognized to be one derivative line of the otherwise extinct theropod dinosaurs (Figure **1**) [25], and the behavioral complexity of those extinct theropods has been a source of considerable speculation. Can we use endocasts of living bird species of varying cognitive ability as a comparative baseline to model the brain properties of extinct theropods derived from endocasts, and then based on endocast comparisons, place different theropods on some scale of cognitive ability? A study on the oldest known fossil bird, *Archaeopteryx*, can illustrate how this can be done. Endocasts of *Archaeopteryx* led to the discovery of several features in its endocranial anatomy that resembled modern birds, including large optic lobes, divided cerebral hemispheres and a relative brain size that is close to some extant bird species [22]. It was concluded that *Archaeopteryx* had the neurological capabilities of powered flight. However, one could similarly take the same data and say, hypothetically, that the endocast properties of *Archaeopteryx* more closely resemble relatively smaller brained extant waterfowl than larger brained extant corvids, and therefore, *Archaeopteryx* had a cognitive ability that would more closely resemble what we see in extant ducks. Theropod endocranial evolution suggests that increases in relative brain size occurred independently many separate times, and therefore, are not limited to *Archaeopteryx* [13]. As such, there exists the exciting possibility of finding comparable brain morphological features in both extant (birds) and extinct maniraptors.

The approach we are suggesting may not be suitable for all theropods, some of which have

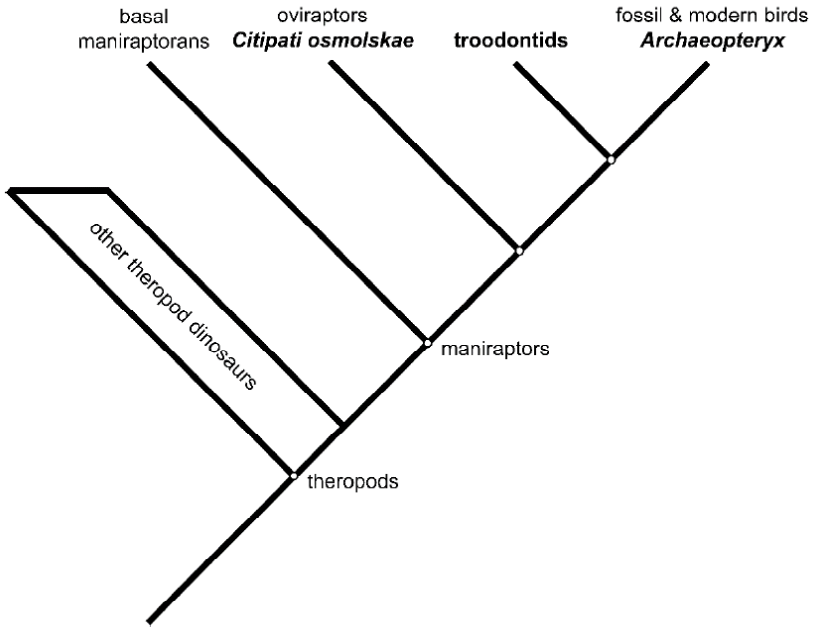

Figure 1: Cladogram showing evolutionary relationships of the derived maniraptoran theropod dinosaurs, including fossil and modern birds. Fossil taxa whose endocasts are compared with living birds in this paper are highlighted with bold text.

endocast properties with no clear equivalent among extant vertebrates. However, derived maniraptoran theropods (such as deinonychosaurs and oviraptorosaurs; see Figure **1**), are thought to have resembled birds, *e.g*., they were small bodied and had feathers, and are generally considered the most behaviorally complex and intelligent of the dinosaurs [11]. Kundrát [26] described the brain (endocast) anatomy of the oviraptor, *Conchoraptor gracilis,* as having a large number of avian characteristics that included expanded cerebral hemispheres and the position of the optic lobes towards the eyes. In addition, its encephalization quotient is similar to some modern bird species. In fact, the *Conchoraptor* endocast was more similar to modern birds than even *Archaeopteryx*! A follow up study on the endocast of *Conchoraptor gracilis* confirmed Kundrát's original conclusions about the inferred avian nature of the oviraptorid brain [14]. Balanoff *et al*. [14] further suggested that the differences between oviraptor and avian brain volumes and encephalization levels are becoming increasingly blurred. Maniraptoran dinosaurs have a brain "Bauplan" that clearly resembles modern birds. Therefore, it follows that comparing the brain-endocast morphology of extinct maniraptors to endocasts of different species of modern birds with characteristically different brain forms, which are known to be associated with different degrees of cognitive ability (*e.g*., high-end crows vs. lower-end ducks), one can generate meaningful hypotheses about the cognitive ability of extinct maniraptors.

APPROACH

The basic approach employed in this study was to create computed tomography images of the skulls of a variety of extant bird species to produce digital brain endocasts whose dimensions could be visualized and quantified. Noteworthy here is that Iwaniuk and Nelson [27] have shown that endocranial volumes can be used as an estimate for brain size in birds. Species we examined included: American robin (*Turdus migratorius*, Order Passeriformes, Family Turdidae), blue jay (*Cyanocitta cristata*, Passeriformes, Corvidae), common nighthawk (*Chordeiles minor*, Caprimulgiformes, Caprimulgidae), American coot (*Fulica americana*, Gruiformes, Rallidae), house sparrow (*Passer domesticus*, Passeriformes, Passeridae), sora rail (*Porzana carolina*, Gruiformes, Rallidae), Canada goose (*Branta canadensis*, Anseriformes, Anseridae), great blue heron (*Ardea herodias*, Pelecaniformes, Ardeidae), double-crested cormorant (*Phalacrocorax auritus*, Suliformes, Phalacrocoracidae), ring-billed gull (*Larus delawarenesis*, Charadriiformes, Laridae), and red-tailed hawk (*Buteo jamaicensis*, Accipitriformes, Accipitridae). It is important to note that the species imaged, although far from exhaustive, see for example the impressive species sample of Iwaniuk and Hurd [28], span a range of brain sizes and endocast dimensions, and that the measured brain dimensions can be loosely correlated with cognitive complexity. For example, the blue jay is a member of the corvid family. Members of the Corvidae are considered by many to display perhaps the richest capacity for learning and possess a most exceptional cognitive ability. By contrast, the Canada goose (Family Anatidae) and the double-crested cormorant (Family Phalacrocoracidae) show considerably less behavioral complexity, and at least compared to corvids, a less exceptional cognitive ability. One specimen of each bird species was obtained from a local wildlife rehabilitation center. Crania were removed and then CT-scanned in the laboratory of Dr. Lawrence Witmer (Ohio University). Digital CT data were visualized using 3D Slicer 4.5 [29].

The endocasts of the sampled bird species were then visually inspected and characterized for shape, with an emphasis on the forebrain/telencephalon, which has been previously studied in theropods [30]. In particular, we measured the ratio of the longest length of the telencephalon to its maximum width (Figure **2**, Table **1**, see Discussion for why this is potentially interesting). Once we calculated this first order measure of the sampled species telencephalic endocasts, we then compared the endocasts with published images of three fossil maniraptoran endocasts from the oviraptor *Citipati osmolskae*, an unnamed troodontid species and *Archaeopteryx* [13]. The question then was which of the sampled extant species of birds had forebrain endocasts that most resembled the extinct species, and then by inference, to what sampled bird species can we look to approximate the behavioral complexity and cognitive ability of the extinct maniraptor species?

RESULTS

An examination of the reconstructed brains of two extinct non-avialian maniraptors and *Archaeopteryx* published in Balanoff *et al*. [13] suggests that, compared to a prototypical modern bird, their forebrains had a higher anterior-posterior length to medial-lateral width ratio; in other words, the brains appeared relatively long and thin (smaller lateral

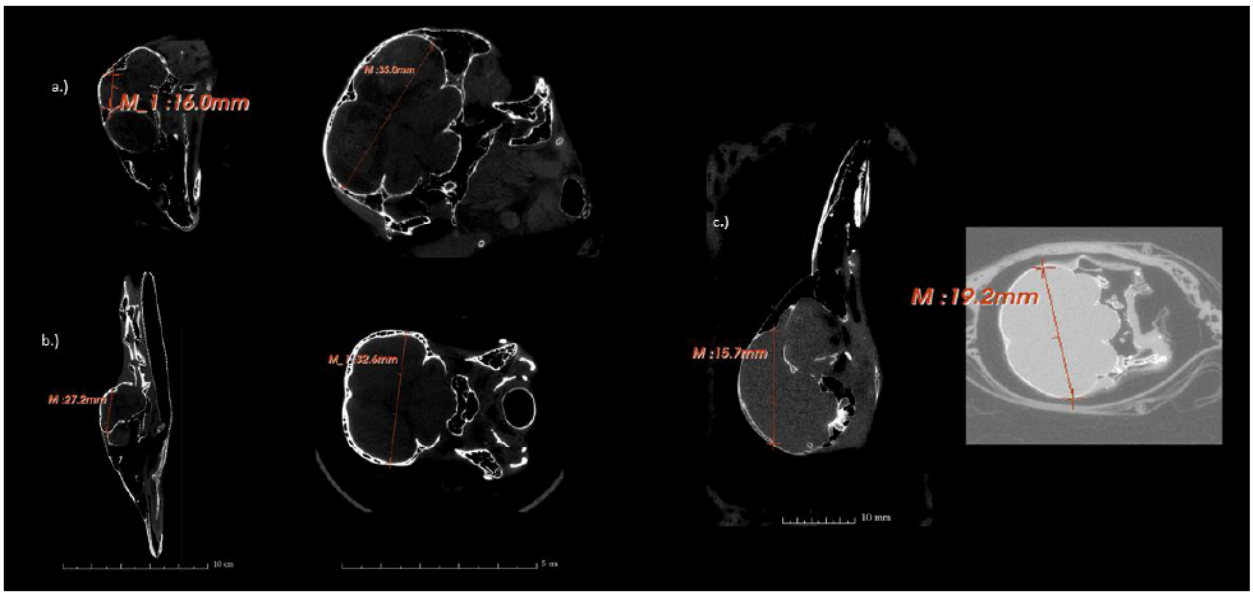

Figure 2: Three examples of how maximum anterior-posterior (sagittal section, left images) and lateral-lateral (coronal section, right images) telencephalic lengths were determined from the digital endocasts of **a**) red-tailed hawk, **b**) Canada goose and **c**) American robin. Lengths (in mm) can be read from the red lines in each image.

extension). None of the forebrains wrapped around the optic tectum in any of the three fossil species. In looking at the digital endocasts of the extant species sampled, what is striking is how similar in shape the endocast of the double-crested cormorant is compared to the endocasts of the extinct maniraptors, especially compared to any of the other extant species we examined (Table **1**, Figure **3**).

Table 1: Ratio of Forebrain Length to Width in Eleven Extant Bird Species

Common Name	Scientific Name	Length (mm)/ Width (mm) Ratio
Double-crested cormorant	*Phalacrocorax auritus*	1.7
Great blue heron	*Ardea herodias*	1.1
American coot	*Fulica americana*	0.99
American robin	*Turdus migratorius*	0.90
Canada goose	*Branta canadensis*	0.83
Ring-billed gull	*Larus delawarensis*	0.82
House sparrow	*Passer domesticus*	0.79
Common nighthawk	*Chordeiles minor*	0.74
Sora rail	*Porzana carolina*	0.73
Blue jay	*Cyanocitta cristata*	0.72
Red-tailed hawk	*Buteo jamaicensis*	0.46

Indeed, an examination of Table **1** reveals that in terms of endocast length to width ratio, the double-crested cormorant, at 1.7, is a notable outlier whose endocast shape seems remarkably similar to the maniraptor endocasts of Balanoff *et al*. [13]. By contrast, the remaining sampled species had length to width ratios ranging from 0.46 to 1.1, and it is not surprising that the blue jay, a corvid, and red-tailed hawk, an adaptive predator, had the lowest length to width ratios indicating they had much wider, laterally extended telencephalons.

DISCUSSION

Our first-order analysis looking at the telencephalic anterior-posterior length to medial-lateral width ratio was inspired by the brain shape of extinct maniraptors [13]. The data suggest that the relatively long and narrow telencephalon of the double-crested cormorant closely resembles extinct maniraptors and that perhaps one can look to cormorants to get an idea of the behavioral complexity and cognitive ability of extinct maniraptors. What is noteworthy is that the cormorant family Phalacrocoracidae first appears in the fossil record relatively early (perhaps by the Campanian, more than 70 million years ago [31, 32]) compared to other extant families of birds, and there are non-controversial, modern-like cormorants recorded from the Oligocene (25 million years ago [33]). Might the ancestral origin of the Phalacrocoracidae be associated with little subsequent change in brain organization?

But what does a “wider” telencephalon mean in terms of specifying the brain areas that may have

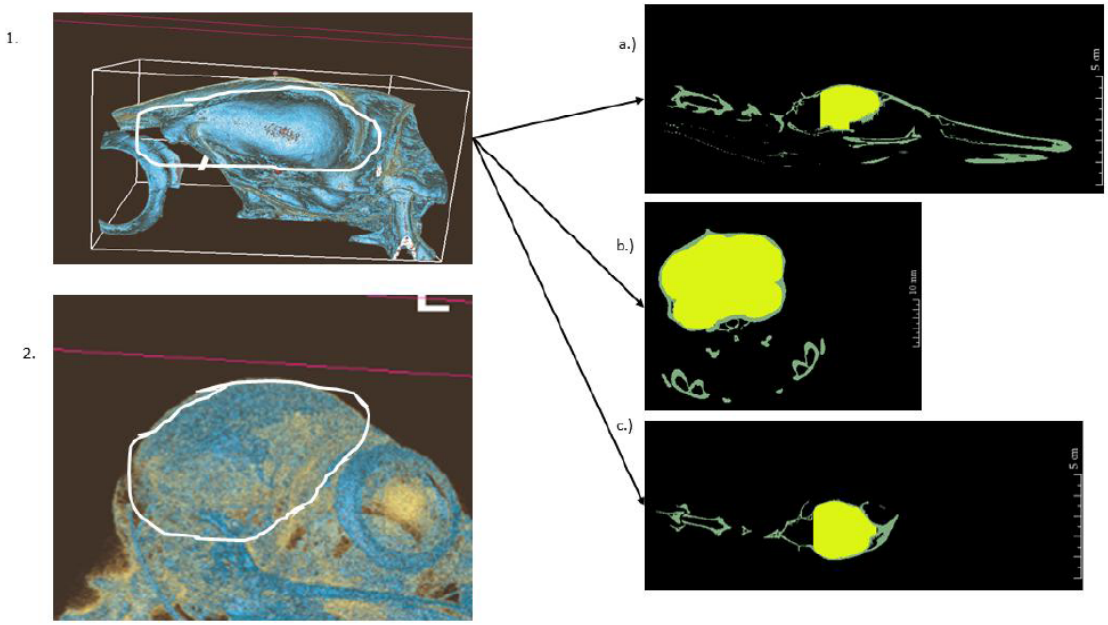

Figure 3: 3D digital renderings of double-crested cormorant (**1**) and blue jay (**2**) skulls. Encircled regions (white lines) reveal the narrower brain of the cormorant compared to the blue jay. Occipital bones are to the left in the cormorant and to the right in the blue jay. The bone is modeled in blue; yellow indicates noise in the data. Subparts **a**, **b** and **c** reveal, in yellow, sagittal, coronal and horizontal sections, respectively, through the cormorant endocast. Green is bony material.

become hypertrophied during avian evolution, a degree of hypertrophy that we speculate may have been diminished in cormorants? Here what appears particularly relevant is the telencephalic region called the nidopallium (see Introduction). Fuchs *et al*. [34] have shown that birds that migrate have smaller telencephalic widths than related species that do not migrate. That difference appears to reflect a smaller nidopallium in migrants compared to non-migrants; a finding which was interpreted to suggest that migrant species are less behaviorally flexible and cognitively less competent. Further, Sayol *et al*. [35] recently reported that much of the variation in telencephalic size in modern birds can be related to differences in the size of the nidopallium. Returning to cormorants, Iwaniuk and Hurd [28] observed that the double-crested cormorant has one of the relatively smallest nidopallium volumes compared to other extant avian species, although Burish *et al*. [36] found that overall relative telencephalic volume in cormorants was low but not close to the lowest among modern birds. Following from these observations, our analysis described above gains a certain validity because it may well be that the nidopallium in cormorants is relatively small, as would be the nidopallium equivalent in the extinct species discussed. Cormorants and extinct maniraptors would share the characteristic of a relatively small nidopallium with suggestive implications for gauging the cognitive ability of the extinct maniraptors. Put another way, the evolutionary lateral expansion of the telencephalon, and therefore presumably the nidopallium, that occurred in other avian lineages, *e.g*., penguins beginning in the Paleocene [37, 38], would have been less robust in cormorants.

Does the exploratory analysis described above mean that the next time a bird watcher goes and observes double-crested cormorants on Lake Erie in the United States that s/he may actually be looking back in time at the behavioral flexibility and cognitive capacity (not any specific behavior) of extinct maniraptors and even *Archaeopteryx*? Obviously such a leap would be premature. The few data we are working with clearly warrant caution in assessing the cognitive ability of extinct maniraptors. It needs to be acknowledged that our analysis was limited to 11 species/species groups, and there may well be other extant avian species with brains that resemble even more the brains of extinct maniraptors. However, what we are confident in saying is that the general approach of endocast comparisons described in this paper is a potentially powerful tool in uncovering the paleontology of cognition. If our approach of using living bird species to gauge the cognitive ability of extinct maniraptors should prove to be useful, then the approach could generalize to other appropriate extant-extinct species comparisons, for example, comparing the endocasts of

modern crocodilians with extinct crocodilians or even ornithischian dinosaurs like *Iguanodon*.

Finally, the raw, digital endocasts we obtained can be subjected to substantially more complex morphometric analyses than what was carried out for this paper. When coupled with appropriate software analyses, computed tomography is a powerful tool that can quantify endocast shape across a number of different dimensions. Clearly future work along the lines we describe will need to go beyond simple visual inspection and crude metrics of shape to provide a multi-dimensional characterization of endocast morphology. In particular, three-dimensional landmarks placed on the digital endocasts can be analyzed via geometric morphometric approaches, including principal components and canonical variates analyses, to determine dimensions of similarity and dimensions of difference among groups.

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